Bats eavesdrop on the sound of copulating flies

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The idea that copulation might increase predation risk is a classic suggestion [1–3], but empirical evidence to support it is surprisingly scarce. While some early work found decreased vulnerability to predation during mating [2], two lab and one very recent field study documented increased predation during mating in freshwater amphipods [4], water striders [5] and locusts [6]. Decreased vigilance, less efficient escape responses, and increased conspicuousness of mating pairs have been suggested as mechanisms that might underpin elevated predation risk during copulation [2]. However, these putative mechanisms have never been investigated empirically. Here we describe a bat-insect system within which copulation greatly increases predation risk. We experimentally demonstrate that wild Natterer's bats (*Myotis nattereri*) 'eavesdrop' on acoustic cues emanating from copulating flies (*Musca domestica*) in a cowshed (Figure 1). With this evidence, we pinpoint increased conspicuousness as a relevant mechanism for elevated predation risk during mating.

When insects sit on vegetation or — as in this case — on the textured shed ceiling, finding them by echolocation is almost impossible. The faint insect echo is fully overlapped and masked by massive echoes from the background [7]. Diurnal flies (Brachycera) typically sit on the substrate at night, and yet they constitute the single most important prey group for Natterer's bats across their distributional range [8] (Supplemental Information). However, it has remained enigmatic how the bats locate the flies. In the study cowshed, even fly movement on the substrate was apparently inconspicuous to the bats, as they never attacked flies that were walking on the ceiling (8986 walking flies filmed across 4 years; Supplemental Information). However, as soon as two flies engaged in copulation, their risk of being attacked by a bat rose dramatically (Figure 1A–C; Supplemental Information). On average, across four observation years, 26% of the flies that engaged in copulation were attacked by the bats (5.3% if all observations are pooled across years; out of 1105 observed copulae, 59 were attacked; Supplemental Information). Thus, the attack rate on copulating flies was strikingly higher than on walking flies (Supplemental Information). The bats did not always manage to actually pick up the copulating flies and sometimes

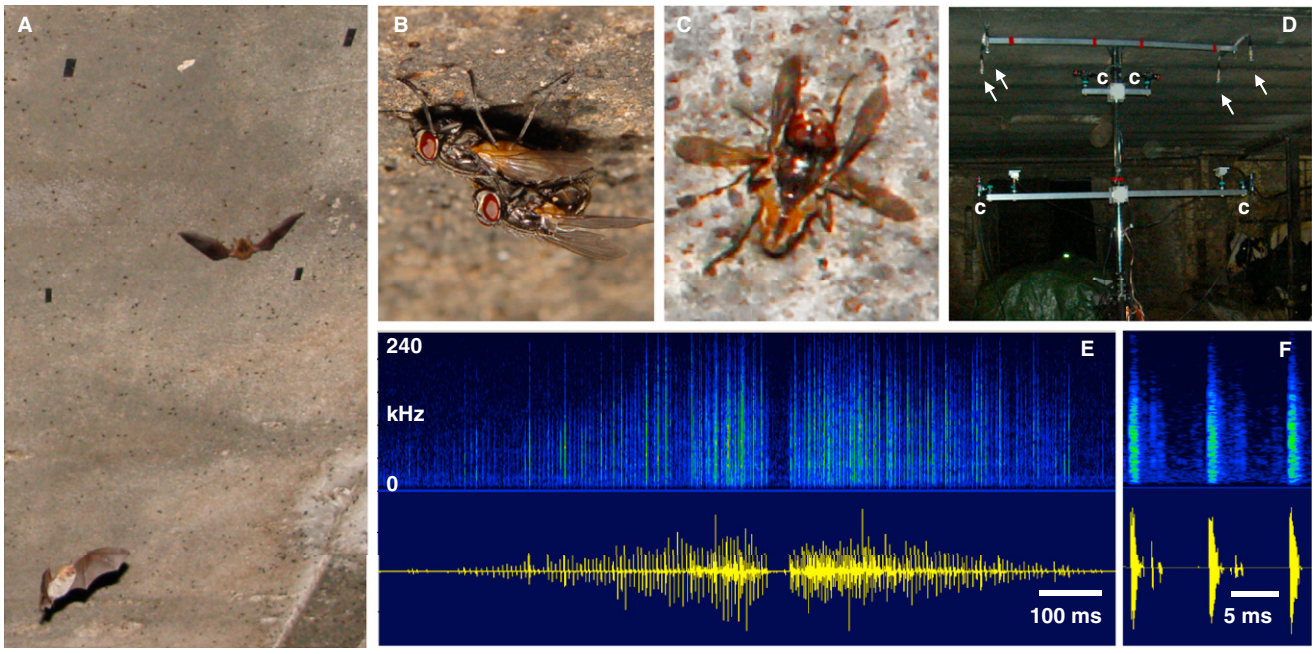

Figure 1. Caught in the act.
(A) Two Natterer's bats foraging for copulating flies in the cowshed. The black dots on the ceiling are sitting flies. The four black tape strips mark an area used for detailed infra-red filming. The upper bat is gleaning flies from the ceiling with its tail membrane (see also Movie S1 in Supplemental Information). (B) A pair of copulating flies on the cowshed ceiling. (C) During copulation, the female (below) holds its wings spread, while the male (top) flutters, which likely produces the buzzing sound. (Photos: S. Greif.) (D) Apparatus used for the playback experiments with wild bats. Four ultrasonic loudspeakers (white arrows) were suspended below the ceiling, while four cameras (white c) and two infra-red light sources were mounted on the same tripod to record the bats' reaction. Note the cow in the background (Photo: E. Kriner). See also Supplemental movie S1, showing a bat attacking an ultrasonic loudspeaker playing fly copulation sounds. (E) Spectrogram (above) and oscillogram (below) of the buzzing sound emitted during the act of copulation. (F) Detail of the same buzzing sequence showing three of the click-like sounds on an enlarged time axis.

missed them by a few millimeters; average success rate was 59%. Out of these successful attacks (n = 39), in only two cases one of the two flies escaped the bat. Therefore, keying in on copulating flies typically afforded the bats with a double meal.

Evidently, the act of copulation removes the flies from the protection against bat echolocation that the substrate echoes provide and makes them conspicuous to the bats. The main cue is likely not the enlarged echo target size, as bats never attacked dead, noiseless fly pairs that we had mounted on the shed ceiling in copula position (n = 35 experimental trials in 2005; each of 15 min duration). In 2008 and 2010, we obtained experimental evidence that the bats eavesdrop on fly copulation sounds instead. When mating, the flies utter a burst of broadband click-like signals, likely from the male's wing-fluttering (Figure 1C,E,F). The 'clicks' contain energy from 9 ± 3 kHz up to 154 ± 22 kHz (peak frequency 41 ± 11 kHz; n = 12 buzzes). They come at a repetition rate of 122 ± 13 s^{-1} (range 105–149 s^{-1}), which is audible as a low frequency buzzing to the human ear. The flies themselves can presumably hear this low frequency buzzing, but not the bat echolocation calls [9]. The sound bursts were 2.65 ± 0.37 s in duration (n = 48). Playback of these fly copulation sounds at naturalistic amplitude through a broadband system (see Supplemental Information) were sufficient to trigger attacks of wild bats in the cowshed (Movie S1 in Supplemental Information). The bats approached, hovered and inspected the speaker, and in several cases tried to glean the acoustically simulated flies from the speaker with their tail membrane — just as they did with real pairs of copulating flies on the ceiling (Figure 1A; Movie S1). This suggests that the flies' copulation sound renders them conspicuous to the bats from a distance. The bats only approached and/or attacked loudspeakers when they played fly copulation sounds (13 approaches in 79 playback trials), but never when playing ultrasonic tones (0 out of 81 playbacks) or noise (0 out of 81) in the same frequency band and amplitude (Pearson Chi-square test χ^2 = 28.2, $p < 0.0001$). Previous attempts of attracting the bats' attention with playbacks of fly sounds that were limited to frequencies below 48 kHz had always failed (2005: 31 playbacks of fly copulation buzzes; 2008: 109 playbacks). This evidence suggests that the bats reacted specifically to the fly copulation sounds as prey cues and that the presence of the very high frequency components are crucial in their search image. This fits the earlier finding that these bats do not attend to insect locomotion noises [8] which have their main energy below 50 kHz [10]. The present evidence for strong response to prey sound above 48 kHz also is in line with the extremely broadband echolocation calls of this species (135 to 16 kHz) [7], which suggest sensitive high frequency hearing to or above 100 kHz. The cowshed afforded us with the rare opportunity to observe and experimentally interact with wild gleaning bats. But we assume that this and maybe other bat species eavesdrop on fly copulation sounds also in forests and meadows; a notion supported by the predominance of diurnal flies in the Natterer's bats' diet across their distribution range ([8] and Supplemental Information).

We here have documented a manifold increase in predation risk in the wild for an insect–mammal system. We identified for the first time a mechanism underlying increased predation on copulating animals: elevated conspicuousness to the predator. The playback experiments identified the sensory channel and the relevant cue. They evidenced that it is the sound of copulation, and especially its high frequency components, that mediate the conspicuousness of copulae to bats. This bears implications for the evolution of mating behavior and suggests a trade-off between repeated or long copulation for successful reproduction and short, inconspicuous copulation for survival. From an evolutionary viewpoint, predators eavesdropping on mate attraction signals constitute a risk for one sex, typically for the courting male (Supplemental Information). Hence, courting despite predation pressure might be viewed as an honest signal of male quality and will thus be under sexual selection (see Supplemental Information). By contrast, if predators attack both male and female during copulation, we would expect strong natural selection against such predation-prone copulation behavior. If both mating partners and all fertilized eggs end up in a predator's stomach, reproductive success is zero.

Supplemental Information

Supplemental Information includes experimental procedures, one table and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.06.030.

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